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Continued decline of the bladderwrack, *Fucus vesiculosus*, in the Archipelago Sea, northern Baltic proper

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Before the 1980s, the bladderwrack (*Fucus vesiculosus*) formed extensive belts along the SW coast of Finland, but already then it began to decline especially in sheltered bays of the inner archipelago. We studied underwater vegetation by scuba diving in 1993–2007. By 2007, six out of eleven sites had lost their *Fucus* belts, and sheltered bays had become refuges for the bladderwrack. In 2006–2007, we studied the effects of temperature, transparency, bottom type, shoreline orientation and location on the bladderwrack distributions and depth penetrations at 61 locations across different archipelago zones. Of these, only location indicated a possible effect.

Introduction

Before the 1980s, the bladderwrack (*Fucus vesiculosus*) had formed extensive belts down to the depths of 10 to 11 m in the Baltic Sea and in the Archipelago Sea of SW Finland (Du Rietz, 1930, Levring 1940, Waern 1952, Haverinen 1954, Andersson 1955, Häyrén 1958, Ravanko 1968, Peussa & Ravanko 1975, Haahtela & Rajasilta 1980, Haahtela & Lehto 1982, Mäkinen *et al*. 1984, Rönnberg *et al*. 1985). It had dominated vegetation biomass on hard bottoms in both the northern Baltic proper and the Archipelago Sea and constituted up to 99% of the total perennial macroalgal biomass and 33%–60% of the total plant biomass (Jansson & Kautsky 1977, Luther 1981, Kangas *et al*. 1982, Kautsky *et al*. 1992, Kautsky 1995). These findings underpin its role as a habitat forming/foundation species that supports the biodiversity of hard bottoms (e.g., Jansson 1972). According to Haahtela (1984) and Kautsky *et al*. (1992) the bladderwrack forms one of the most diverse habitats in the Baltic Sea.

During the 1980s, the bladderwrack declined and disappeared from several locations (Kangas *et al*. 1982, Haahtela 1984, Pliński & Florczyk 1984, Mäkinen *et al*. 1984, Kautsky *et al*. 1986, Nilsson *et al*. 2004). This caused a shift from submerged vegetation dominated by perennial *F. vesiculosus* to a predominance of annual algae. Several authors discussed its decline and how it affected changes in animal abundance and biomass, as well as cascading effects on higher trophic levels and biodiversity (Kraufvelin & Salovius 2004, Lauringson & Kotta 2006, Wikström & Kautsky 2007). Biodiversity is the central theme in the European Marine Strategy Framework Directive (MSDF 2008) and places the bladderwrack in a special position in environmental monitoring programs (Rohde *et al*. 2008, Rinne *et al*. 2011, Kraufvelin *et al*. 2012).

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Indeed, the bladderwrack is already included in some national monitoring programs (e.g., Nilsson *et al*. 2004, Schories *et al*. 2009, Rinne 2014).

A number of factors can explain the distribution and depth penetration of the bladderwrack in the Baltic Sea. According to Waern (1952), the amount of light available for photosynthesis explained the deepest occurrence of individual bladderwrack specimens in the Baltic Sea. Kautsky *et al*. (1986) suggested that with increased eutrophication, the depth penetration of light decreases over time. This restricts the bladderwrack belts closer to the shores. Later studies proposed e.g., competition (Torn *et al*. 2006, Kraufvelin *et al*. 2007), grazing by herbivores (Haahtela 1984, Hemmi *et al*. 2004, Nilsson *et al*. 2004), as well as induced chemical defences (Jormalainen & Honkanen 2008, Weinberger *et al*. 2011) as affecting distribution of *F. vesiculosus*. In the early 1980s, Kangas *et al*. (1982) suggested that factors linked to eutrophication act together. Effects of submergence and seawater salinity (Remane & Schlieper 1974, Serrão *et al*. 1996a, Rinne *et al*. 2011, Nyström-Sandman *et al*. 2013, Johansson 2013), as well as stress by ice scouring (Kiirikki 1996a) or wave action (Kiirikki 1996b, Serrão *et al*. 1996b) were also studied. Finally, adaptation was not ruled out as an explanation for the bladderwrack distribution in the Baltic (Johansson 2013).

Our objectives were: (1) To test the effects of environmental factors (*see* below) on temporal and spatial distribution of the bladderwrack in southwestern Finland. Global climate change may affect the bladderwrack due to increasing temperatures, increase in windiness in coastal areas, decrease in salinity, and progressing eutrophication (*see* e.g., Hänninen *et al*. 2000, BACC 2008, Anonymous 2011, Nyström-Sandman 2011, Rinne *et al*. 2011, Wallin *et al*. 2011, Kraufvelin *et al*. 2012, BACC2 2015). Our long-term studies (1993–2000), with 11 vegetation monitoring transects used for comparison, gave us the possibility to ponder the relations between the bladderwrack and its changing environment. (2) To test the previously-presented hypothesis that the depth penetration of the bladderwrack populations provides a simple method to assess benthic habitat quality (Kangas 1985, Kautsky *et al*. 1986, Bäck 1998, Rinne *et al*. 2011). This hypothesis would be supported if, as suggested by Pitkänen (2004), in the outermost Archipelago Sea the bladderwrack belts are denser, have greater depth penetration and are generally less affected by eutrophication than in the more nutrient-enriched inner areas. Therefore, the bladderwrack occurrences along 61 hard-bottom transects were studied together with environmental variables in 2006 and 2007. (3) To test the hypothesis that shoreline orientation affects bladderwrack abundance (Luther 1981, Kiirikki 1996c, Ruuskanen *et al*. 1999). Shorelines facing towards the southwest, which is the prevailing wind direction in the area, together with increased exposure may provide better growing conditions for the bladderwrack (Bäck & Ruuskanen 2000). This leads to denser populations with higher biomass as well as plant morphology typical to exposed shorelines (Kautsky *et al*. 1992, Kiirikki 1996b, Ruuskanen *et al*. 1999, Wallin *et al*. 2011). We suggest that the effect of ship-generated waves, next to the fairways, should have a comparable effect (Roos *et al*. 2004). We also propose that light conditions should differ between northern and southern slopes and generally favour bladderwrack settlements on the southern slopes of islands. We tested those hypotheses in an orientation study that compared exposure, prevailing wind directions and distances to fairways with the bladderwrack belt occurrences along shores with different orientations.

Material and methods

The study area

The Finnish Archipelago Sea covers an area of 10 000 km^2 in SW Finland (Fig. 1) and is a part of the northern Baltic Sea. There are over 22 000 islands with more than 14 000 km of shoreline (Granö *et al*. 1999). The area is non-tidal and shallow with an average depth of 23 meters (Jumppanen & Mattila 1994). This complicated landscape may be broadly divided into inner, middle, and outer archipelago zones (e.g., Jaatinen 1960). This zonation is also reflected in littoral shores across the study area, where the

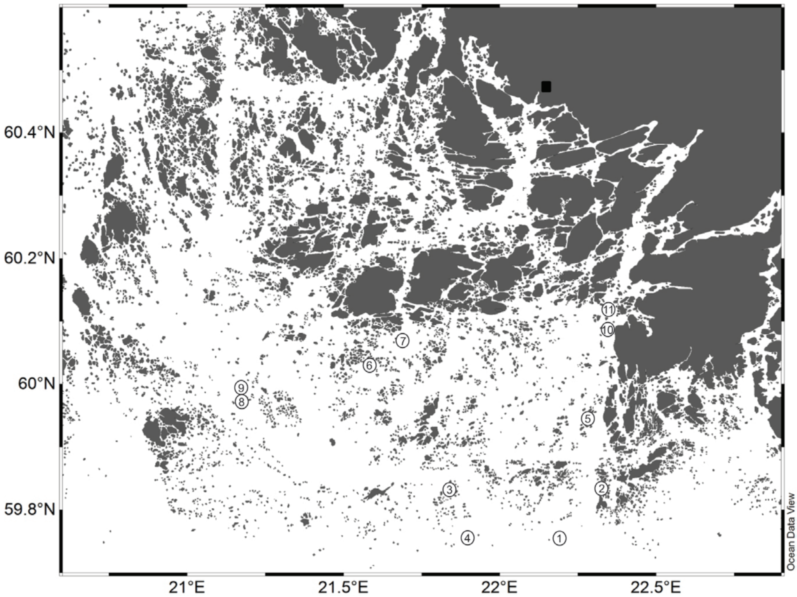

Fig. 1. Long-term monitoring locations of *Fucus vesiculosus* on the Finnish SW coast, founded in 1993–1994.

inner Archipelago shores are characterized by high amounts of clay and silt, while the middle zones consist more of boulders and secondary till deposits. The outer parts are mainly rocky. In total, over half of the shorelines are rocky, and together with till comprise almost 90% of the shoreline (Granö *et al*. 1999). Surface water salinity ranges from 2 PSU at the innermost reaches to around 6 PSU at the southern fringes of the area [although a value of 8 PSU was reported at the turn of the century by Pitkänen (2004)]. The low salinity, ranging from 5 to 7 PSU (also called the critical salinity, or the horohalinicum, *see* e.g., Remane and Schlieper 1971), prevents many marine and limnic species from establishing themselves in the area and this results in a relatively low species diversity. The area is characterized as extremely sensitive to eutrophication and suffers from serious nutrient over-enrichment (Pitkänen 2004). During the late summer of 2005, the average total phosphorus content in surface waters was 20 μg l^{-1} while the value measured near the city of Turku equalled 80 μg l^{-1} (Suomela & Sydänoja 2006). Areas of upwelling between the Archipelago Sea and the Baltic proper (Pitkänen 2004) cause occasional nutrient inflows to the Archipelago Sea, resulting in mass occurrences of filamentous algae (Kiirikki 1996a, Vahteri *et al*. 1997). Water temperatures in the study area range from < 0 to < 25 °C. During the winters between 1961 and 1990, the ice cover persisted on average for 115 and 43 days in the inner and outer archipelago, respectively (Seinä & Peltola 1991).

The long-term study

In 1993/1994, 11 transects were established in order to reveal temporal changes in the bladderwrack belts (Figs. 1–3) (Vahteri *et al*. 1997). They were revisited in 2000/2001 (Karvonen *et al*. 2002), and 2006/2007 (this study). The fieldwork was carried out by scuba-diving. The starting point of each was marked with paint on the shore and photographed. The orientation of each transect was recorded, and on the first visit, the end of each transect underwater was marked either with a painted rock or with a white canister filled with rocks. Each study transect was investigated by extending a 50 m rope (marked at 1 m intervals) on the bottom perpendicular to the shoreline. The depth of each meter marked on the rope was recorded together with bottom and vegetation types. The transect was further divided into four vegetation zones: filamentous algae, the bladderwrack belt, vascular plants, and red algae (Vahteri *et al*. 1997). The percent-

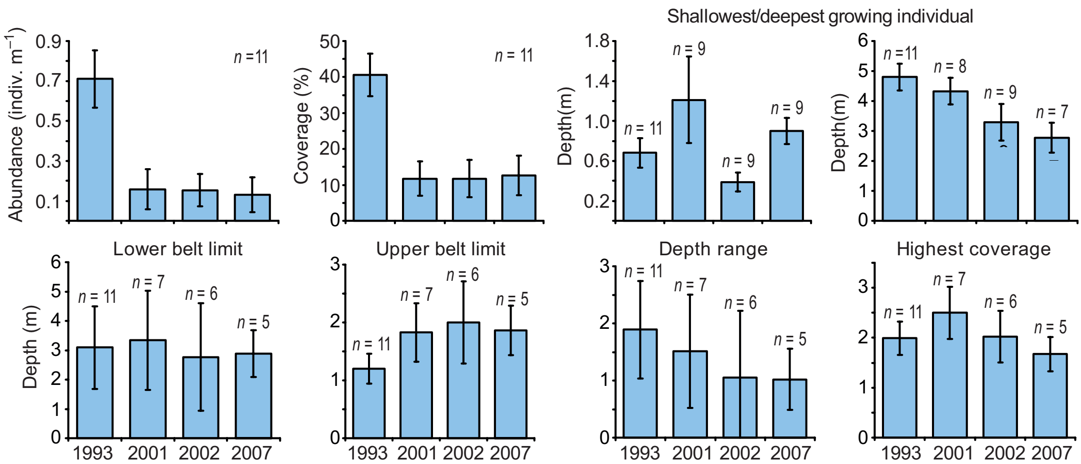

Fig. 2. Measured (mean ± SD) characteristics of the bladderwrack distribution on the Finnish SW coast (northern Baltic Sea) 1993–2007. The annual abundance and coverage (%), were calculated for all transects (n = 11). Upper and lower belt limits, depth range, highest coverage and shallowest and deepest growing *Fucus* individuals were only calculated for transects with complete *Fucus* belts.

age cover of each algal species inside a 1-m^2 frame, subdivided into 100 smaller squares (100 cm^2) was documented. The squares were placed randomly at three locations in each vegetation zone either on top or beside the transect. Additional data collected from the bladderwrack belt included the depth of the shallowest and deepest growing individuals, upper and lower depths of the continuous bladderwrack belt (over 10% coverage), and the estimated optimum growing depth (highest coverage). The estimated average coverage of the bladderwrack belt was further calculated as the average of all squares recorded within the continuous bladderwrack belt. Later observations of the long-term underwater vegetation transects were done according to Bäck (1998) and this proved to be directly comparable to the methods used previously. In order to compare the results between different slope profiles the *abundance of the bladderwrack* was calculated as *depth range* (i.e., lower minus upper limits of the continuous *F. vesiculosus* belt) × *average coverage*. Theoretically, this projects all study transects to a vertical screen, where each meter on the study transect would correspond to one meter in a vertical direction. Since we took the depth range as the difference between two depth readings, the correction for water level changes at the time of monitoring was not necessary.

Distribution of the bladderwrack

During 2006 and 2007, 61 diving transects were studied (methods according to Bäck 1998). All long-term study transects (Fig. 1) were used, with 50 new transects added to cover the whole area (Fig. 4 and Appendix 1). The principle of site selection was to cover the area with three approximately parallel study lines running across the Archipelago Sea from north to south. The westernmost study line extended from Mynälahti southwest, the center study line started from the city of Turku, with the eastern study line reaching from Paimionlahti to Örö. The studies were conducted during late summer, from July to August. Data were collected the same way as described in the previous chapter. Additional (environmental) data collected at the time of the sampling included water temperature measured at 1 m depth, Secchi depth, as well as bottom type at the typical growth depth (base rock or stones) of the bladderwrack. The average and maximum fetches were later estimated for each study transect according to Suominen *et al*. (2007). In order to study possible effects of ship traffic on the bladderwrack, distances to the fairways used by large ships were also measured using maps. Fairways were divided into those used by merchant ships and those by ferries travelling between Finland and Sweden. We also recorded if the fairway was in direct contact with the study sites or was instead shielded by shallower areas or islands. In addition, to study differences along the east–west gradient, the study sites were distinguished by the three study lines they resided on, and by numbering each transect from north to south to study the changes along the north–south gradient. Finally, each station was given a value to correspond with its location comparable to Jaatinen's division (Jaatinen 1960) of the archipelago zones based on land-to-sea ratio.

The effects of shore orientation

The notion that denser populations with higher biomasses and a typical morphology exist on exposed shorelines (Kautsky *et al*. 1992, Kiirikki1996b, Ruuskanen *et al*. 1999, Rinne 2011) was tested at 25 study sites during the autumn of 2007 (Fig. 5). The locations studied were initially selected on a map. Each location was a small island, which was studied by scubadiving along five study transects (numbered 1 to 5) extending perpendicular from the shoreline to directions of 0°, 72°, 144°, 216° and 288°, respectively.

Statistical analyses

As a uniform null hypothesis, we assumed no difference between response variables in temporal or spatial comparisons. All the tests in this study were performed using the statistical program SPSS ver. 22 (IBM Corp., Armonk, NY). Differences were considered significant at $p < 0.05$.

For the temporal studies, the General Linear Model (GLM) Repeated Measures procedure was used. This procedure provides analysis of variance (ANOVA) when the same measurement is made several times on each subject or case. Prior to analysis the data were tested for sphericity as assumed by repeated measures ANOVA and if needed the Greehouse-Geisser correction was used. The response variable was explained by sampling time (year). The response variables used were: abundance, percentage cover, shallowest and deepest growing individuals, lower and upper limit of the continuous bladderwrack belt, and depth of the highest coverage.

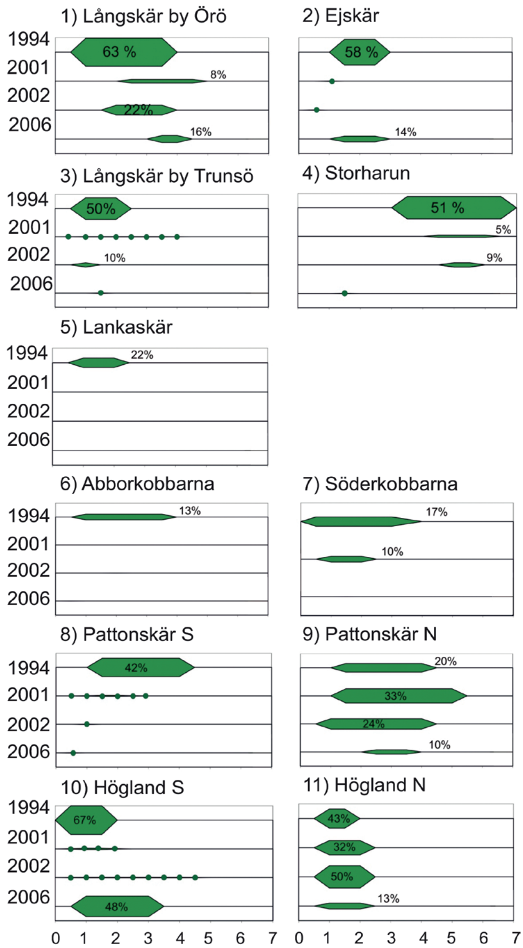

Fig. 3. Depth profile changes in the bladderwrack belts at eleven study sites on the Finnish SW coast (northern Baltic Sea) between 1993 and 2007. The *x*-axis value is depth range (m) and the bar width is the percentage coverage. Green circles indicate individual plants. The locations are roughly grouped into southernmost (and outermost zone): the Långskär Skerries by Örö (1) and Trunsö (2) Islands, Ejskär (3), Storharun (4), and Lankaskär (5) Skerries, westernmost (and middle archipelago): the Islets of Abborrkobbarna (6) and Söderkobbarna (7), the southern and northern Pattonskär Skerries (8 and 9) and northern (innermost inner archipelago zone): the southern and northern Högland Islands (10 and 11).

For spatial studies, both regression analysis and ANOVA for one dependent variable by one or more factors and/or variables were used. Prior to ANOVA the normality was tested using the

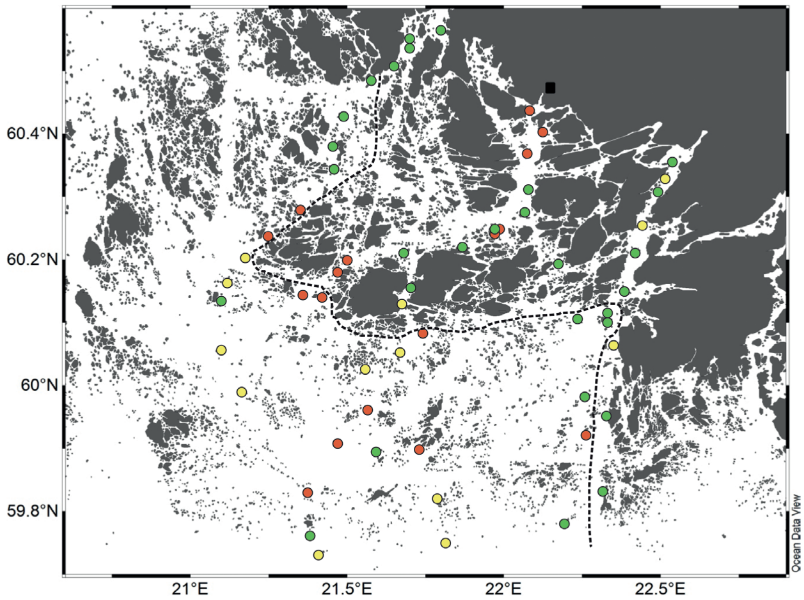

Fig. 4. Results of the spatial *F. vesiculosus* study on the Finnish SW coast (northern Baltic Sea) during 2006 and 2007. Green shows locations with the bladderwrack belts, yellow indicates individual plants and red marks the absence of *F. vesiculosus*. The approximate borderline between the outer and middle archipelago according to Jaatinen (1961) is marked with a dashed line.

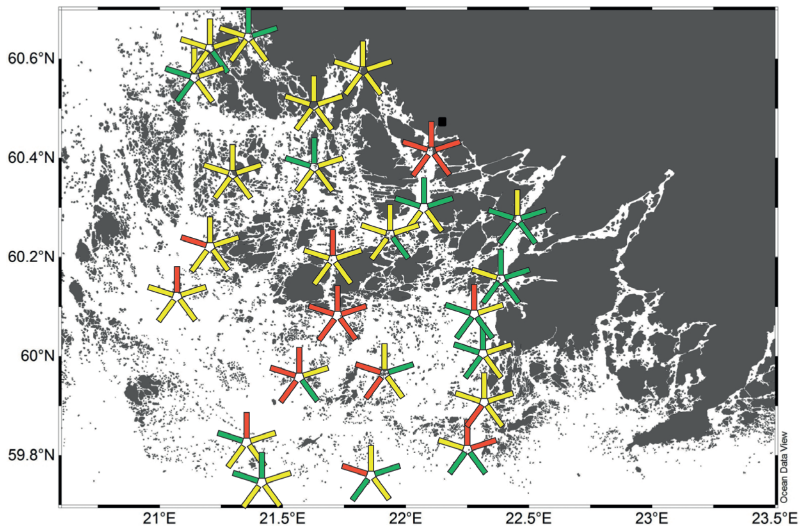

Fig. 5. Locations for studies of shoreline orientation of the bladderwrack on the Finnish SW coast (northern Baltic Sea) in 2007. Red indicates transects with no bladderwrack, yellow indicates transects with individual plants and green marks transects with continuous belts.

Shapiro-Wilk test and the variances randomness was tested using Levene's test. In the regression analysis, the Hosmer and Lemeshow test was used to test the models fit to the available data. The presence/absence of a bladderwrack belt, abundance, the lower limit of a continuous bladderwrack belt, and deepest growing individuals were each used as dependent factors being explained by the available environmental factors and variables.

For shoreline orientation tests, Pearson's χ^2-test was first performed to reveal possible differences between the transects. The Linear Mixed Models procedure in SPSS expands the GLM such that the data are permitted to exhibit correlated and non-constant variability. This procedure was used to investigate differences between different shore's orientations such that the transects were considered correlated. For the dependent factor, the abundance of the bladderwrack, and the lower depth limit of the bladderwrack belt were used to be predicted by the transect numbers.

Results

Long-term changes

In 1993 and 1994, bladderwrack belts were found at each transect of the eleven study sites. During the 14 years covered by the present study, continuous bladderwrack belts disappeared from 6 of the 11 transects, with complete disappearance of *F. vesiculosus* from 3 transects. The abundance of *F. vesiculosus* in the bladderwrack belts (depth range × percent coverage) decreased significantly from 0.71 to 0.13 between the years 1993 and 2001 and remained low thereafter (Fig. 3 and Table 1). The coverage (%) of the bladderwrack also decreased significantly after the first study year and remained low (Fig. 2 and Table 1) while lower and upper limits of individuals showed only negligible changes. Lower and upper limits of belts, depth range and highest coverage were excluded from the analysis due to low *n*. The smallest changes in depth (Fig. 3) were found at the innermost study sites, e.g. on the island of Högland: those were the only sites where the bladderwrack belts remained unchanged during the entire study period. Six of the studied eleven transects that lost their continuous belts (Fig. 3) were situated in the outer archipelago areas.

Distribution of the bladderwrack

Although individual plants and sites without *F. vesiculosus* were found in the outer Archipelago Sea, the bladderwrack belts were found in the middle and inner areas, with the exception of areas off Turku (Fig. 4). While most of the studied environmental factors (temperature, bottom type at typical growing depth, average and maximum fetch) failed to show a statistically significant effect, both the Secchi depth and proximity to large shipping fairways were statistically significant in predicting the characteristics of the bladderwrack belts (Fig. 4). Nevertheless, the significant result of the Hosmer and Lemeshow test of the model's lack of fit implied that the model fits poorly to the available data (Table 2). Therefore, abundance, depth range, coverage of the bladderwrack, and the north–south position of the study site in the study line in the GLM univariate ANOVA were unable to explain the characteristics of the bladderwrack.

Effects of shore orientation on the bladderwrack

No statistically significant differences were found between the different shore orientations

Table 1. Characteristics of the bladderwrack populations in the Archipelago Sea of Finland. Results of the repeated measures ANOVA with number of tested cases, test of sphericity, degrees of freedom, F values, and significance.

Response variable	*n*	Mauchly's test of sphericity	df	*F*	*p*
Abundance	10	0.030, Greenhouse-Geisser correction used	1.897	6.934	0.007
Coverage percentage	10	0.007, Greenhouse-Geisser correction used	1.590	13.761	0.001
Shallowest growing individual	7	0.394, sphericity assumed	3	1.810	0.181
Deepest growing individual	5	0.641, sphericity assumed	3	1.483	0.269

Table 2. Logistic regression analysis of occurrence of the bladderwrack belts in the Archipelago Sea area.

Predictor	*B*	SE	Wald's χ^2	df	*p*	Odds ratio
Constant	0.119	1.006	0.014	1	0.906	1.126
Distance to shipping lane	0.106	0.39	7.529	1	0.006	1.112
Secchi depth	–0.602	0.341	3.119	1	0.077	0.548
Test			χ^2	df	*p*	
Overall model evaluation			10.495	2	0.005	
Goodness of fit (Hosmer and Lemeshow test)		21.742	8	0.005		

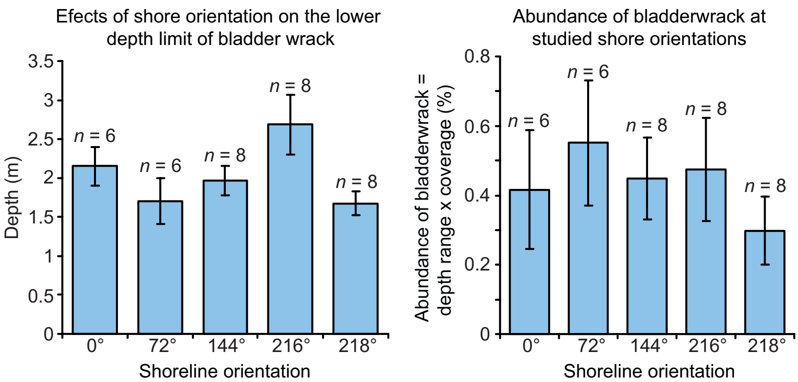

Fig. 6. The effects of shoreline orientation on the abundance and the deeper depth limit (mean ± SD) of the bladderwrack belts in the on the Finnish SW coast (northern Baltic Sea) in 2007.

as factors explaining *F. vesiculosus* distribution (Table 3, Figs. 5 and 6). In running the Linear Mixed Model Procedure, the iteration was either stopped before convergence or the resulting matrix did not reach positive values. Therefore, we conclude that shoreline orientation in the Archipelago Sea did not reveal any observable pattern in the bladderwrack characteristics (Figs. 5–6 and Table 3).

Discussion

There are numerous studies stating that the decline of the bladderwrack in the Archipelago Sea started in the 1970s (e.g., Luther 1981, Haahtela 1984, and Kangas *et al*. 1982). This decline evidently continued during this study period, and our findings are supported by the studies in the adjacent Bay of Bothnia (Snickars *et al*. 2014). Our monitoring studies showed a marked decline of the bladderwrack in the outer archipelago. Six out of eleven transects studied lost the continuous bladderwrack belts. In terms of *F. vesiculosus* abundance, there was a reduction of over 81%. This is a marked reduction in a predominant species that still occupied virtually all hard bottom environments in the study area at the beginning of the 1990s (Fig. 2). Moreover, the depth ranges and coverage (%) of the bladderwrack also declined, with the latter showing a decrease from 40% in the beginning of the 1990s to approximately 13% during the study period. This led to sporadic spatial growth, as well as the loss of the species from some study sites.

Although the possible environmental factors contributing to the observed decrease in coverage (%) are both physical and biological, including eutrophication, light conditions, grazing, etc., weighing their relative importance in a field study as ours would be excessive. Even though a simple relation between eutrophication, light conditions and the bladderwrack success was assumed initially by Kautsky *et al*. (1986), the role of light is still under discussion. Torn *et al*. (2006) demonstrated the possible existence of a different mechanism in various parts of the Baltic Sea. Other effects such as grazing on *F. vesiculosus* that has shifted the ecosystem to a less desirable state due to a general nutrient increase (Haahtela 1984, Worm *et al*. 1999, Nilsson *et al*. 2004). Furthermore, shading by filamentous algae and increased sedimentation caused by excessive primary production may

Table 3. Results of Pearson's χ^2 test of the effects of shoreline orientation to the bladderwrack belts.

	χ^2	df	p
Transect orientation for *F. vesiculosus* abundance categories (absent, individuals, belt)	5.979	8	0.650
Line orientation to two *F. vesiculosus* categories (the bladderwrack belt or not)	5.000	4	0.287

hinder the recruitment and settlement of fucoids (Eriksson & Johansson 2003, Kraufvelin *et al.* 2007). Recent increases in filamentous algae biomass (Kiirikki & Blomster 1996, Vahteri *et al.* 2000) may have led to increased competition pressure on the bladderwrack in the Archipelago Sea. Further changes could also be induced by sedimentation (Isaeus *et al.* 2004), competition with filamentous algae (Isaeus *et al.* 2004, Wikström & Pavia 2004), difficulties in the bladderwrack reproduction (Jönsson 2004), and grazing pressure (Hemmi & Jormalainen 2002, Weinberger *et al.* 2011). Recent studies (Johansson 2013) even bring species adaptation into focus. We suggest some further environmental factors that could be added to the list presented above, such as overgrowth by filamentous algae, increased filamentous algae growth on the substrate under the bladderwrack belt, diseases of the bladderwrack, declining salinity of the Archipelago Sea area, increased average wind conditions (BACC 2008, BACC2 2015), and/or ship-generated waves. It is clear that interconnections among these factors add a great complexity to the overall picture (e.g., Kangas *et al.* 1982) and render it extremely difficult to pinpoint the most important ones. Despite this great complexity, eutrophication and light still form the focus of recent studies. Although eutrophication of the Archipelago Sea area continued generally over the study period (Suomela & Sydänoja 2006, Anonymous 2011), there was variation among different archipelago zones. Our result may be explained by several factors but most likely they are to be found among documented environmental changes in the Archipelago Sea, such as decreasing salinity, decreasing loading of P and N from the fish farms in the middle Archipelago Sea, decreasing P and chlorophyll-*a* concentrations and increasing Secchi-visibility in the surface water in the inner Archipelago Sea, which all are reported by the regional environmental office (Anonymous 2011). For example, fish farming has decreased in the Archipelago Sea to the extent that its P loading, which was about 50 tonnes yearly, is today only around 30 tonnes.

Despite statistically insignificant changes in other variables measured (the upper limit of the bladderwrack belt evidently moved from 1.2 to 1.9 m depth and the depth of the deepest growing plants in the study transects seemingly decreased during the study period from 4.8 to a 2.8 m depth) we suggest that those also are indicative of the same phenomenon, which suggest further studies on the topic with more effort in field sampling.

The depth of the deepest growing plants in the study transects steadily decreased during the study period. Often these individuals grew on top of boulders or cliffs, which are clean microhabitats free from the surrounding sediments (Kiirikki 1996b). Together with worsening light conditions, sedimentation steadily increased. These factors favour individual bladderwrack plants to inhabit shallower areas although the competition with filamentous algae is more intense there (Vahteri *et al.* 2000).

The distribution study produced surprising results. It has previously been shown that the bladderwrack forms the most extensive belts in the middle and outer Archipelago Sea (Rönnberg *et al.* 1985). That was not the case in our study. Compared with the situation in the 1980s (Rönnberg *et al.* 1985), the pattern of occurrences we found was reversed. In the 1980s, the most extensive belts were found in the outer Archipelago on almost all hard surfaces, excluding only sheltered and eutrophic bays (Luther 1981). By comparison, these sheltered bays are currently important places harbouring the bladderwrack, while most of the outer Archipelago is devoid of it, with the largest numbers of continuous bladderwrack belts being found in the inner and middle parts of the Archipelago Sea. Our results resemble those by Nilsson *et al.* (2004) and Kautsky *et al.* (2011), who documented corresponding reverse changes over time, possibly indicating improving environmental conditions for *F. vesiculosus* in the middle archipelago.

Although our original aim was to separate areas where the bladderwrack communities are thriving, based on the observations, those areas were scarce and far apart. The environmental factors tested in order to explain the characteristics of the bladderwrack zones produced a valid model, however the explanatory value of the model was poor (Table 2). Only the position of the studied sites along the north–south gradient seemed to have some indicative value, suggesting further studies.

The decline of the bladderwrack has continued in the innermost Archipelago, particularly near the city of Turku. This decline was first described by Andersson (1955) and was further studied by Peussa and Ravanko (1975). Andersson first described *F. vesiculosus* communities around the island of Ruissalo and while the bladderwrack still formed continuous belts along the island's western shoreline in 1975 (Peussa & Ravanko, 1975), it was evidently decreasing. In 1985, Rönnberg *et al*. (1985) described the Turku area situation to be almost identical as in 1975. In the present study, the closest bladderwrack belts to Turku were found in the Grangrundet area, over 5 km south of the study area of 1975. The closest single bladderwrack plants were observed near Järvistensaari, over three kilometres from those observed in 1985. However, we did not actively look for individual bladderwrack plants. Therefore, our view may be too pessimistic. Conversely, in the Paimionlahti area, the innermost bladderwrack boundaries would seem to occur on the same islets where it was observed in 1955.

The effects of the shore orientation were unexpected. The results of this study showed that, in the Archipelago Sea, there were no differences in the probability of the bladderwrack being more frequent at any shoreline orientation. This result would imply that there is no difference on which side of an island the surveillance transects for the bladderwrack should be established. The bladderwrack populations vary along different shore orientations (Luther 1981, Kiirikki 1996a, Ruuskanen *et al*. 1999) and it has been hypothesised that shorelines facing towards the dominant prevailing SW wind directions, together with increased exposure, would provide better growing conditions (Bäck & Ruuskanen 2000). These conditions have promoted denser populations with higher biomasses and a typical morphology on exposed shorelines (Kautsky *et al*. 1992, Kiirikki1996b, Ruuskanen *et al*. 1999, Wallin *et al*. 2011). We also suggested that the effect of ship-induced waves next to the fairways should have a comparable effect and that light conditions should differ between northern and southern slopes, generally favouring the bladderwrack settlements on the latter. Our results, however, show no reason draw such generalisation over the Archipelago Sea and the differences between our results and those cited above might be based on the mosaic nature of the Archipelago Sea environment as compared with the more homogenous coastal area of the Gulf of Finland.

Conclusions

The decrease that already started in the 1950s has continued to the present day. *Fucus vesiculosus* populations have crashed even on hard bottoms in the outer Archipelago Sea, and the species is no longer actively competing for living space, but is rather struggling for survival. In order to maintain at least the current biodiversity levels within the Archipelago Sea, the remaining bladderwrack communities must be given the best possible protection. In an open aquatic environment, it is almost impossible to protect a single species or its habitat. The protection schemes and programs must, therefore, protect the whole environment and prevent eutrophication. The loss of *F. vesiculosus* from the Archipelago Sea would lead to lower biomasses of many associated floral and faunal species, resulting in a decrease in production that would probably affect higher trophic levels (Wikström & Kautsky 2006). Further studies should be directed to aid the reproduction success of the remaining populations and artificial resettling of the bladderwrack communities to the areas that it previously occupied.

Numerous bladderwrack studies have brought forward numerous factors affrcting its distribution patterns and temporal changes. Nevertheless, despite detailed local studies and advances in modelling approaches (e.g., Schories *et al*. 2009, Alexandritis *et al*. 2012, Nyström-Sandman *et al*. 2013), the generality of findings is quite poor and a theoretical background for studies of *Fucus*–environment relationships has not developed beyond a basic background connection to light and eutrophication. The relation to eutrophication, although evident, is far from simple, because it is accompanied by several other factors, such as grazing and inducible defences (Hemmi *et al*. 2004, Nilsson *et al*. 2004, Jormalainen & Honkanen 2008, Weinberger *et al*. 2011), as well as effects of light (e.g., Rohde *et al*. 2008) and possibly even submergence (Torn *et al*. 2006). The effects of predicted global climate change, which include, especially for the Baltic Sea (BACC 2008, BACC2 2015), expected increases in freshwater runoff, a decline in salinity, and an increased nutrient leaching, may play a role in the future development of *F. vesiculosus* vegetation (Torn *et al*. 2006, Kraufvelin *et al*. 2012, Johansson 2013, Rinne 2014) and complicate the picture even further.

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Appendix 1. Results of the spatial study of the bladderwrack in the Archipelago Sea area, Finland. The transect and station numbers for each Island. Lower = maximum depth (m) of the bladderwrack belt, Coverage = percentage cover, Range = belt depth range (m), Abundance = calculated depth range (lower minus upper limits of the continuous *F. vesiculosus* belt) × average coverage**)** of the bladderwrack (those stations with individual plants are marked with 0.001), Secchi = Secchi disc depth and Bottom = type of hard bottom existing at the bladderwrack growing depths (1 = rocky, 2 = stones).

Transect	Station	Island	Lower	Coverage	Range	Abundance	Secchi	Bottom
1	1	Aaviikki	0.9	50	0.2	0.100	1.8	2
1	2	Kråkholmen	0	0.5	0	0.001	2.3	2
1	3	Lökholmen	1	18.33	0.4	0.073	2,1	2
1	4	Brinkholm	0	0.25	0	0.001	2.4	2
1	5	Stora Tjuvholmen	1.1	40	0.7	0.280	2.2	2
1	6	Brännholm	2	6.08	1.4	0.085	2.2	2
1	7	Långskär	2.7	58.75	2	1.175	2.2	2
1	8	Högland N	1.8	12.67	0.8	0.101	2.5	1
1	9	Högland S	3	47.5	1.9	0.903	2.5	1
1	10	Norrlandet	1.2	59.25	0.5	0.296	3.2	1
1	11	Långsidan	0	0.25	0	0.001	2.3	2
1	12	Ljusskär	3.3	76	2.6	1.976	3.2	2
1	13	Högsåra	1.4	29.33	0.9	0.264	3.5	2

continued

Appendix 1. Continued.

Transect	Station	Island	Lower	Coverage	Range	Abundance	Secchi	Bottom
1	14	Lankaskär	0	0	0	0	3.1	2
1	15	Ejskär	2.4	13.6	0.8	0.109	3.2	1
1	16	Långskär/Örö	3.8	16.67	0.5	0.083	4.3	2
2	1	Iso-Kaskinen	0	0	0	0	1.4	2
2	2	Kuuva	0	0	0	0	1.0	2
2	3	Vepsä	0	0	0	0	1.6	1
2	4	Grangrundet	2.1	70	1.4	0.980	2.0	2
2	5	Västra Lindsor	2.3	10	1	0.100	2.2	2
2	6	Jäimäluoto	0	0	0	0	2.2	2
2	7	Seili 18	3.4	50	2.3	1.150	3.0	1
2	8	Seili 12	0	0	0	0	2.8	1
2	9	Seili 4	0	0	0	0	3.0	1
2	10	Lilla Sådik	2.3	23.33	1.5	0.350	2.5	1
2	11	Svartholm	0	8	0	0.001	2.8	2
2	12	Pärnäinen	2.1	70	1.1	0.770	2.8	2
2	13	Fagerholm	0	0.25	0	0.001	2.4	2
2	14	Gunnkobbarna	0	0	0	0	3.5	2
2	15	Bärskär	0	0.25	0	0.001	3.0	1
2	16	Abborkobbarna	0	0.25	0	0.001	3.4	1
2	17	Ingolskär	0	0	0	0	3.5	1
2	18	Vidskär	0	0	0	0	3.7	1
2	19	Mossaskär	3.2	3.6	1.5	0.054	5.1	2
2	20	Bodö	0	0	0	0	4.8	2
2	21	Västergaddarna	0	0	0	0	4.0	1
2	22	Långskär/Trunsö	0	0.25	0	0.001	3.2	2
2	23	Örö bådan	5	26.67	0.6	0.160	3.1	1
2	24	Storharun	0	0.25	0	0.001	4.1	1
2	25	Lillharun	0	0.25	0	0.001	3.4	1
3	1	Tuomo	1.3	11	0.4	0.044	1.0	2
3	2	Rahkio	1.6	4	0.8	0.032	1.3	2
3	3	Kalmanhohde	1.2	14.33	0.6	0.086	1.3	1
3	4	Nahkaluoto	0.9	14	0.4	0.056	1.2	2
3	5	Harjalliset	1.7	10.06	1	0.101	1.7	1
3	6	Maarluoto	2.7	1	1.7	0.017	2.2	1
3	7	Getholm	1.6	3.06	0.6	0.018	2.6	2
3	8	Biskopsö	1	2	0.4	0.008	2.6	2
3	9	Furuskär	0	0	0	0	2.2	1
3	10	Kalvholm	0	0	0	0	2.4	1
3	11	Hallmanskär	0	0.25	0	0.001	2.8	2
3	12	Furuskär	0	0	0	0	2.0	2
3	13	Rönnören	0	0	0	0	3.0	2
3	14	Sundbådan	0	0.25	0	0.001	3.0	1
3	15	Roskär	0	0	0	0	3.6	2
3	16	Stora Skarpen	0	0	0	0	3.0	1
3	17	Bredskär	3.3	23.33	0.6	0.140	3.1	2
3	18	Stora Korpskär	0	0.25	0	0.001	2.9	1
3	19	Pattonskär N	3.4	9.71	1.1	0.107	3.8	2
3	20	Pattonskär S	0	0.25	0	0.001	3.1	1